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Karyotype differentiation in the endemic subterranean Mole rats of South Africa (Rodentia, Bathyergidae)

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Abstract

Analyzed karyotype differentiation in 3 genera and 4 currently accepted species of African mole rats, Bathyergidae. The species and subspecies examined and in parenthesis the sample size (N) and the diploid chromosome numbers (2n) are: *Cryptomys hottentotus hottentotus* (N = 5, 2n = 54), *Cryptomys hottentotus natalensis* (N = 8, 2n = 54), *Cryptomys hottentotus damarensis* (N = 2, 2n = 74 and 78), *Georychus capensis* (N = 7, 2n = 54), *Bathyergus suillus* (N = 1, 2n = 56) and *Bathyergus janetta* (N = 1, 2n = 54). The results suggest that karyotypically, 2n = 54 is shared by all species except *C. h. damarensis* and *B. suillus* and karyotypic evolution is distinct in both diploid numbers and in karyotype morphology. We conclude that bathyergids are not karyotypically conservative, and display prolific speciation involving chromosomal evolution.

Introduction

Prolific speciation of subterranean rodents has occurred over all major continents and has given rise to an unusually large number of species. Chromosomal differences are frequently associated with different species, a common pattern in rodents (Patton and Sherwood 1983) including subterranean rodents (Nevo 1979). However, while karyotypic differentiation is well documented for most families of subterranean rodents, little is known about the Bathyergidae, an endemic family of subterranean rodents in Africa (Matthey 1956; George 1979; Capanna and Merani 1980; William et al. 1983). Based on the karyotypic analysis of two bathyergids, George (1979) suggested chromosomal conservatism for the Bathyergidae in contrast to other subterranean rodents, such as the genera *Ctenomys*,

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Thomomys, Geomys and *Spalax,* which display distinct karyotypic diversity (see details in Nevo 1979). This suggestion prompted us to make a more extensive chromosomal study of the bathyergids.

The history of the systematics of the Bathyergidae has been recently reviewed by de Graaff (1979). It was characterized by both extreme lumping (Ellerman et al. 1953) and extreme splitting (Roberts 1951). Three genera and four species of mole rats are currently recognized as occurring in South Africa. These are the Cape dune mole rat, *Bathyergus suillus,* the Namaqua dune mole rat, *Bathyergus janetta,* the Cape mole rat *Georychus capensis,* and the Common mole rat, *Cryptomys hottentotus.* Of the latter species, 3 subspecies are recognized (de Graaff 1979), i.e. *C. h. hottentotus, C. h. natalaensis* and *C. h. damarensis.* We present here karyotypic evidence for all these taxa, also supported by allozymic variation (Nevo et al. 1985), suggesting that the species splitting approach to systematics is biologically more realistic than the lumping of species. Our evidence also suggests that the idea of a karyotypic conservatism in the bathyergids may be an oversimplification. While some bathyergid species may show morphological similarity in their diploid numbers, others show more dynamic differentiation in both diploid number and in karyotype morphology.

Material and methods

The karyotype analyses of 19 bathyergids comprising 3 genera and 4 species were performed. Species, localities and ecological remarks are given in the Table and the distribution of collecting sites in Fig. 1.

Somatic metaphase plates were obtained from bone marrow preparations following the usual air-drying procedure suggested by Hsu and Patton (1967); meiotic figures were studied in air-drying preparations from testis tissues according to the method proposed by Evans et al. (1964). A standard staining was carried out using 4 % Giemsa in phosphate buffer at pH 7. G-bands were induced by Trypsin digestion according to Seabright (1971); C-bands were produced by treatement with Ba $(OH)_2$ according to Sumner (1972) as modified by Bickham (1979). Nucleolar organizer regions (NOR's) were analyzed by the silver method of Howell and Black (1980).

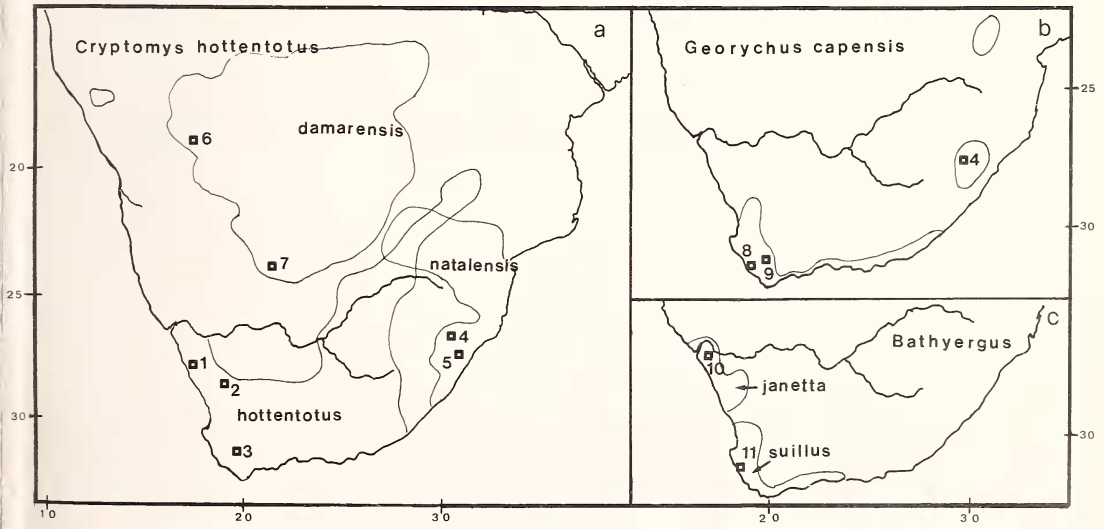

Fig. 1. Distributional areas of the South African species of bathyergids investigated in the present paper. a: *Cryptomys hottentotus;* b: *Georychus capensis* and c: *Bathyergus janetta* and *B. suillus.* Thin lines mark the limits of the ranges of the species and subspecies; squares indicate the collecting sites: 1 = Komaggas; 2 = Eendekuil; 3 = Rawsonville; 4 = Nottingham Road; 5 = Pietermaritzburg; 6 = Otjiwarongo, 7 = Kalahari Gemsbok National Park; 8 = Cape Town; 9 = Du Toits Pass; 10 = Oranjemund; 11 = Swellendam

Species studied, collecting sites and ecological remarks

Species	N	Sex	Localities	Latitude and longitude coordinates	Ecological remarks
Cryptomys hottentotus hottentotus	1	F	Eendekuil, S.W. Cape	32° 42′ S, 18° 53′ E	Agricultural field on sand, shale and silt substrate
	4	F	Eendekuil, S.W. Cape		
	1	F	Komaggas, North Cape	29° 48′ S, 17° 30′ E	Sandstones with Acacia trees
	1	F	Near Rawsonville, S.W. Cape	32° 42′ S, 19° 15′ E	Sandstone and clays near farms
Cryptomys hottentotus natalensis	1	F	Pietermaritzburg, Natal	29° 36′ S, 30° 22′ E	Grassland on >50% clay, shallow soils overlying shale near the campus of the University of Natal
	2	M	Pietermaritzburg, Natal		
	3	F	Pietermaritzburg, Natal		
	4	M	Pietermaritzburg, Natal		
	1	F	Nottingham Road, Natal	29° 22′ S, 29° 52′ E	Grassland on >50% clay, moist, humic soils overlying red soil on dolerite
Cryptomys hottentotus damarensis	1	F	Otjiwarongo, Northern S.W. Africa	20° 27′ S, 16° 42′ E	Consolidated red Kalahari sands
	1	M	Two areas of the Kalahari Gemsbok Nat. Park	26° 28′ S, 20° 34′ E	Kalahari dunes, vegetated
Georychus capensis	1	F	Du Toits Pass, S.W. Cape	33° 44′ S, 19° 6′ E	Sandstones near highway, Du Toit Pass
	2	F	Du Toits Pass, S.W. Cape		
	3	F	Du Toits Pass, S.W. Cape		
	1	M	Nottingham Road, Natal	29° 22′ S, 29° 59′ E	See above
	1	F	UTC Cape Town	33° 56′ S, 18° 28′ E	Red clay soil near the campus of the University of Cape Town
	1	F	UTC Cape Town		
Bathyergus janetta	1	M	Oranjemund, Orange River	28° 33′ S, 16° 24′ E	Cultivated alluvial sands and arenosols
Bathyergus suillus	1	F	Swellendam, East Cape	34° 1′ S, 20° 27′ E	Cultivated arenosols, soft sands

Results

Bathyergus janetta (Thomas and Schwan, 1904)

One male was investigated displaying a 54 chromosome karyotype (autosomal fundamental number, aFN = 104); all chromosomes are biarmed (metacentrics and submetacentrics according to the nomenclature of Levan et al. 1964,). The X heterochromosome is a large metacentric, the Y is acrocentric (Fig. 2). It is difficult to subdivide the chromosomes of the karyotype into classes because of their progressive decrease in size and of light differences in their centromeric index.

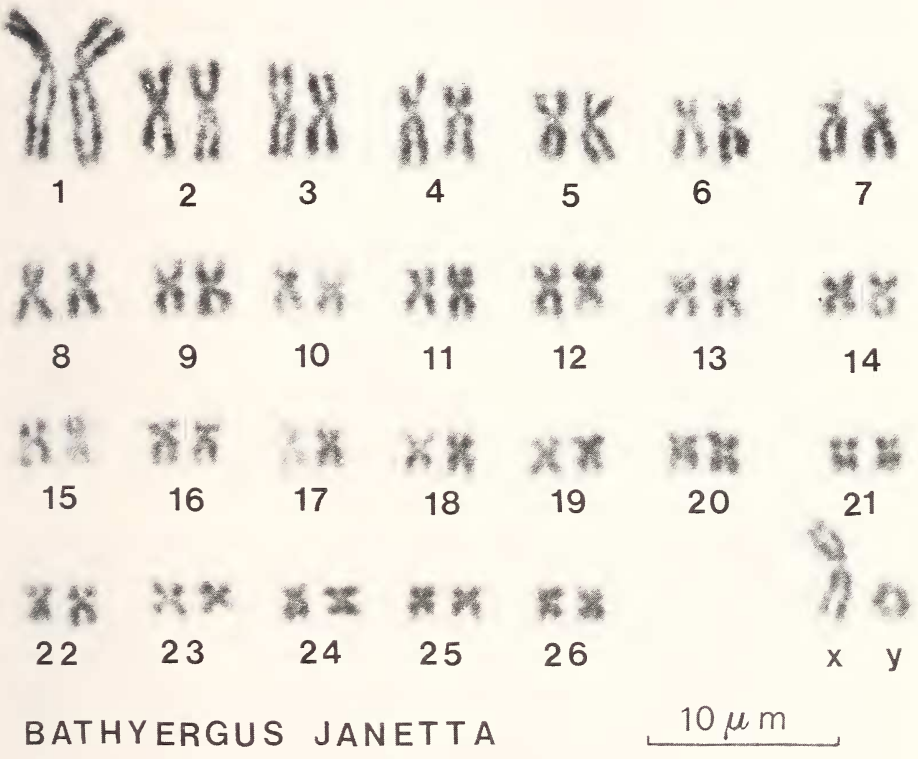

Fig. 2. Karyotype a of male *Bathyergus janetta*

Silver reaction revealed 2 pairs of small metacentric nucleolar chromosomes carrying siver dots (NOR's) in interstitial position on the long arm (Fig. 3). Meiotic diakinesis reveals 27 bivalents and among them the X–Y sex bivalent can easily be identified by its peculiar shape with the small Y paired end-to-end to a large X-chromosome (Fig. 4).

Bathyergus suillus (Schreber, 1782)

One female was studied. This specimen displayed a 56 chromosome complement (aFN = 102) (Fig. 5). The first 7 autosomal pairs show a certain gross morphological homology in comparison with those of *Bathyergus janetta;* a pair of metacentrics may be identified as

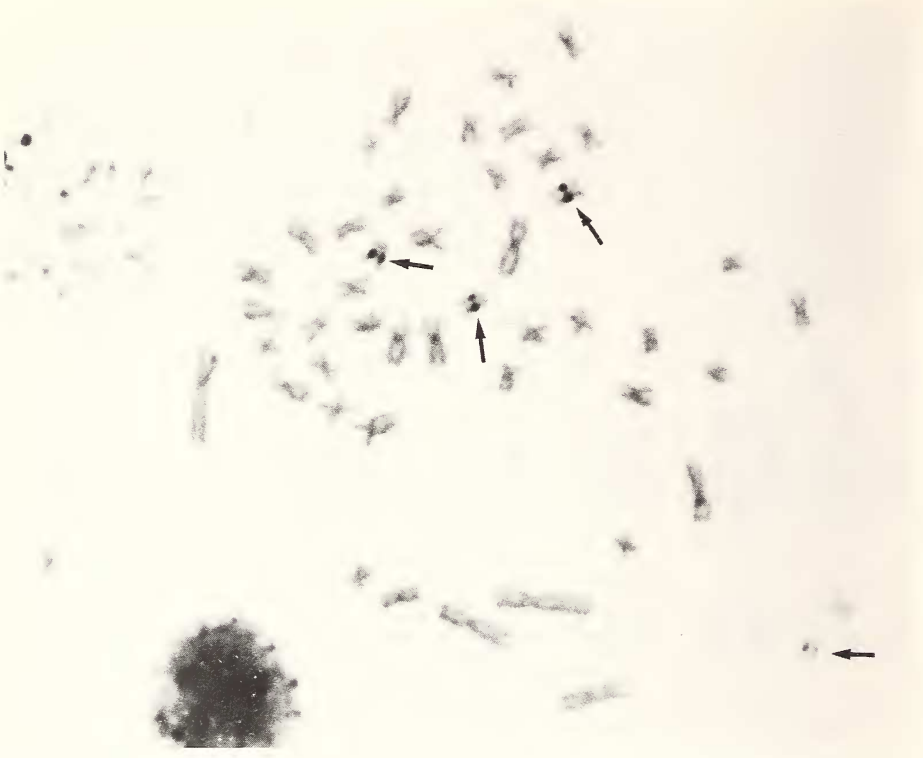

Fig. 3. Metaphase of *Bathyergus janetta* stained according to the silver method for the NORs. Arrows indicate four small biarmed chromosomes displaying clear silver spots (NORs) in intercalary position

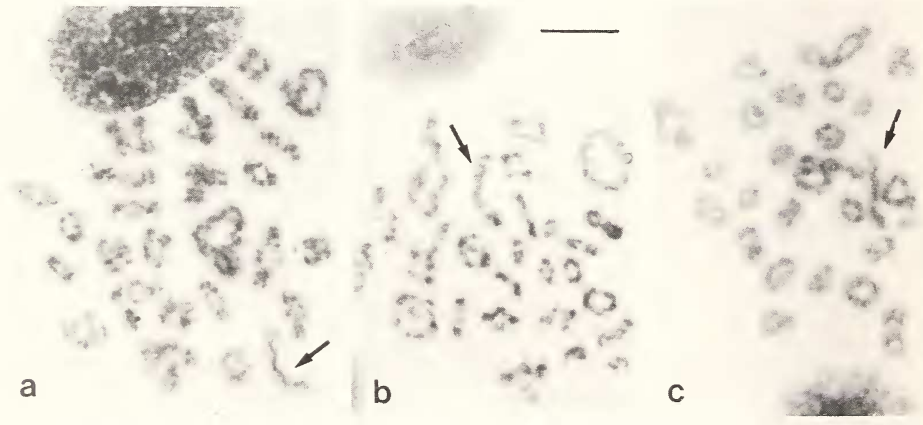

Fig. 4. Meiotic diakyneses of a: *Bathyergus janetta;* b: *Georychus capensis;* c: *Cryptomys hottentotus natalensis.* 27 bivalents can be observed for each species. Arrows indicate the X–Y sex bivalent. The line at the top of Fig. b corresponds to 10 μm

the X chromosome pair because of similarity to those observed in *B. janetta.* The chromosomal pairs 8 and 11 are subtelocentric and acrocentric, respectively, which do not find homology in the *B. janetta* karyotype. The rest of the karyogram consists of small metacentrics and submetacentrics. Chromosome pair 25 is acrocentric, showing a clear

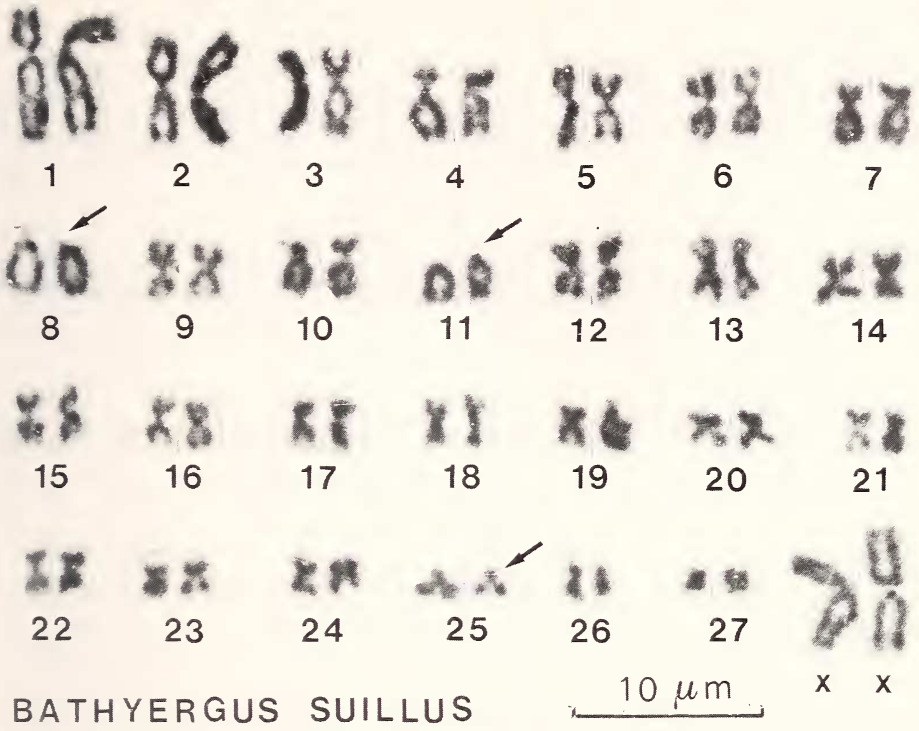

Fig. 5. Karyotype of a female *Bathyergus suillus;* arrows indicate the acrocentrics characterizing the karyotype of this species

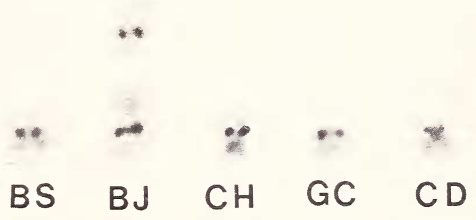

Fig. 6. The nucleolar chromosomes of *Bathyergus suillus* (BS), *B. janetta* (BJ), *Cryptomys h. hottentotus* (CH), *Georychus capensis* (GC) and *Cryptomys h. damarensis* (CD). Only one chromosomes of each pair is represented. Notice the two biarmed chromosomes of *B. janetta* displaying intercalary paracentromeric silver dots. Magnification 3,000 X

heteropicnotic paracentromeric band which corresponds to the silver dots evidenced by the NOR's method. In *Bathyergus suillus,* only one pair of acrocentric chromosomes possesses a NOR's band in a paracentromeric position (Fig. 6).

Georychus capensis (Pallas, 1778)

One male and four females were studied from 3 localities (see Table). The Nottingham Road *G. capensis* are geographically isolated from the Cape populations (see Fig. 1). The diploid number of this species is 2n = 54 (aFN = 100), confirming previous observations by Matthey (1956). Most autosomes are metacentrics and submetacentrics except two

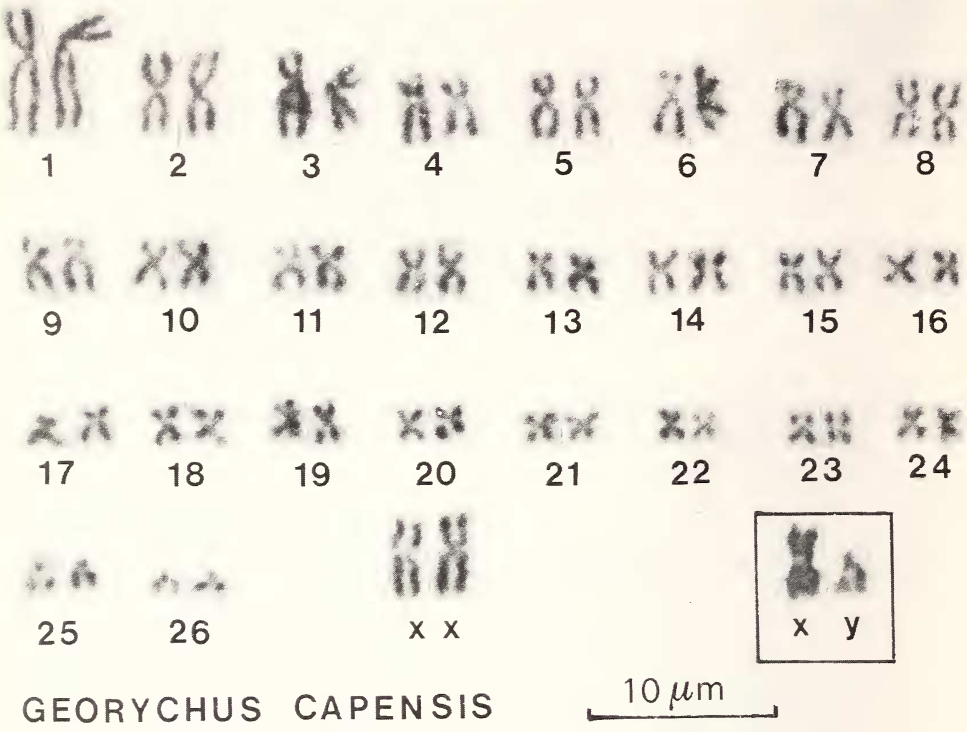

Fig. 7. Karyotype of female *Georychus capensis.* The male heterochromosomal complement from another individual is boxed in the lower right corner

pairs of small acrocentrics, the smallest in the karyogram (Fig. 7). One of these shows an heteropicnotic area which corresponds to the NOR's obtained by the silver procedure (Fig. 6). The X heterochromosome is a large metacentric and the Y is medium sized subtelocentric. This unusual size of the Y chromosome in *Georhycus capensis* was also remarked on by MATTHEY (1956). An unusually large Y chromosome was recorded in *Heterocephalus glaber* by CAPANNA and MERANI (1980).

Five pairs of chromosomes show clear C-bands, namely a. a large metacentric showing a large centromeric C-band b. a large submetacentric displaying two bands, one in the centromeric area and one in the telomeric one, c. a medium size metacentric displaying a centromeric band, d. a medium size submetacentric showing a large paracentromeric C-band in the long arm and e. a small metacentric showing the short arm entirely heterochromatic (Fig. 8).

Cryptomys hottentotus (Lesson, 1862)

Four females belonging to the nominal subspecies *C. h. hottentotus* (Roberts, 1913) and 2 males and 3 females belonging to the subspecies *C. h. natalensis* (Roberts, 1913) have been studied. The two above mentioned subspecies show a similar karyotype consisting of 54 chromosomes (Fig. 9 and 10); nonetheless some morphological differences can be identified. The third and fifteenth chromosomal pair of the karyogram arranged in decreasing size are metacentrics in *C. h. hottentotus,* while they are submetacentric and subtelocentric respectively (centromeric index 25 in chromosome no. 3 and 14 in no. 15) in *C. h.*

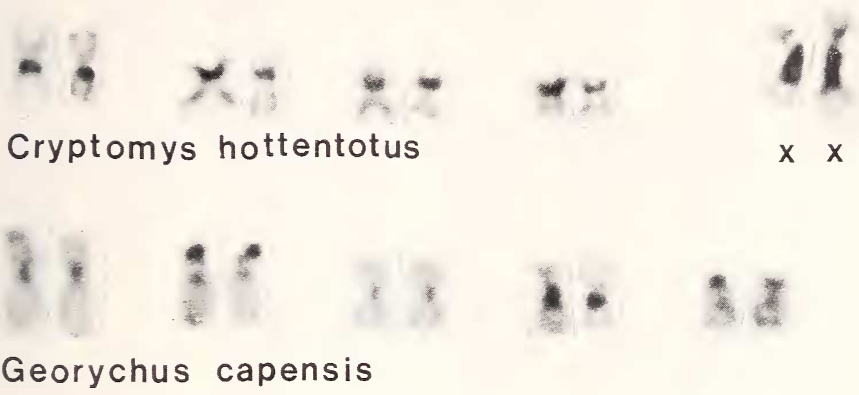

Fig. 8. A comparison of the distribution of heterochromatic masses (C-bands) is compared between *Cryptomys hottentotus* and *Georychus capensis.* Notice the different pattern displayed by the two species

natalensis. The remaining chromosomal pairs display equal morphology in size and shape in both subspecies; consequentely the aFN of *C. h. hottentotus* is = 102, while in *C. h. natalensis* is = 100. A distinct peculiarity of both karyotypes is a small subtelocentric chromosomal pair which have a poorly stained short arm (no. 26 in both karyograms). This latter is stained by the silver reaction for the NOR's bands (Fig. 6). The sex chromosome pair, identified in the male *Cryptomys hottentotus natalensis* karyotype, consists of a large X submetacentric chromosome (centromeric index 26) and a small acrocentric Y. The X heterochromosome has a large C-band in the paracentromeric area of the long arm (Fig. 8). Such a C-band is also evident in a submetacentric pair (centromeric index 34) of *C. h. hottentotus* which we have, accordingly, identified as the X chromosome of this subspecies.

Two *Cryptomys hottentotus damarensis* (Ogilby, 1838) from widely separated localities were studied, one from Otjiwarongo was analyzed by bone marrow procedure, the other from Kalahari Gemsbok Park by spleen tissue culture (done in Cape Town by M. Howard-Tripp). The specimen from Otjiwarongo had a karyotype of 2n = 74 chromosomes, whereas the Kalahari one had 2n = 78. The latter had 16 biarmed autosomes (8 pairs) and a large metacentric X-chromosome, the remaining chromosomes include both small and large acrocentrics (Fig. 11).

Discussion

Chromosomal sibling species, based on Robertsonian whole-arm rearrangements and/or pericentric inversion and reciprocal translocation are widespread in unrelated subterranean herbivore mammals (Nevo 1979 and references therein). To date over 30 karyotypes have been described for *Spalax* (2n = 38–72. FN = 74–124), 3 karyotypes of *Myospalax* (2n = 44–64, FN = 80–108); 6 karyotypes of *Ellobius* (2n = 17–54; FN = 34–60); over 20 karyotypes in *Thomomys talpoides* and *Geomys* (2n = 38–72; FN = 68–102); for *Pappogeomys* (2n = 36–46; FN = 66–86) and for *Ctenomys* 11 karyotypes have been described out of the 60 known species (2n = 22–68; FN = 44–122).

In contrast to the above karyotypic diversity, George (1978) suggested that bathyergid molerats were karyotypically conservative. This was based on her findings that both *Heterocephalus glaber* and *Heliophobius argenteocinereus* had karyotypes with a diploid

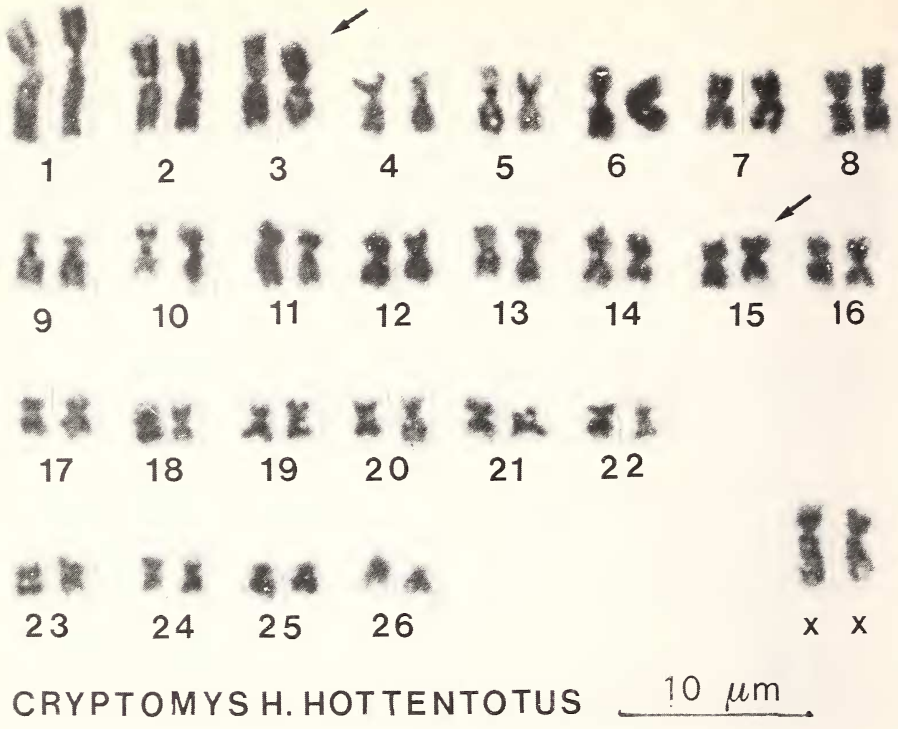

Fig. 9. Karyotype of a female *Cryptomys hottentotus hottentotus.* The arrows indicate the chromosomal pairs 3 and 15 which are morphologically different in *Cryptomys h. natalensis* (see Fig. 10)

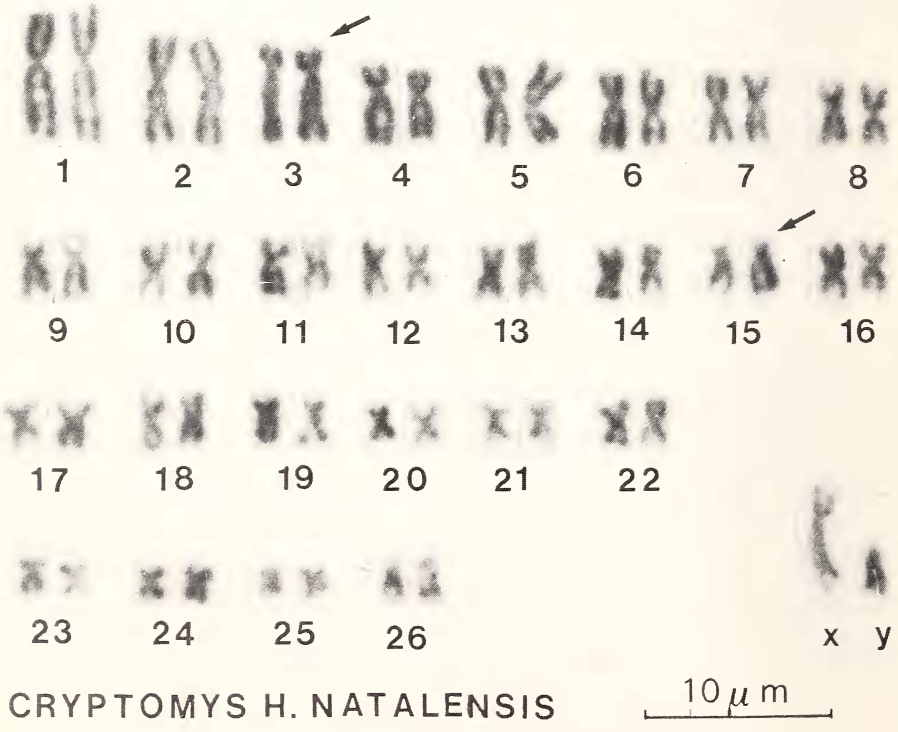

Fig. 10. Karyotype of a male *Cryptomys hottentotus natalensis.* The arrows indicate chromosome pairs 3 and 15 which are morphologically different in *Cryptomys h. hottentotus* (see Fig. 9)

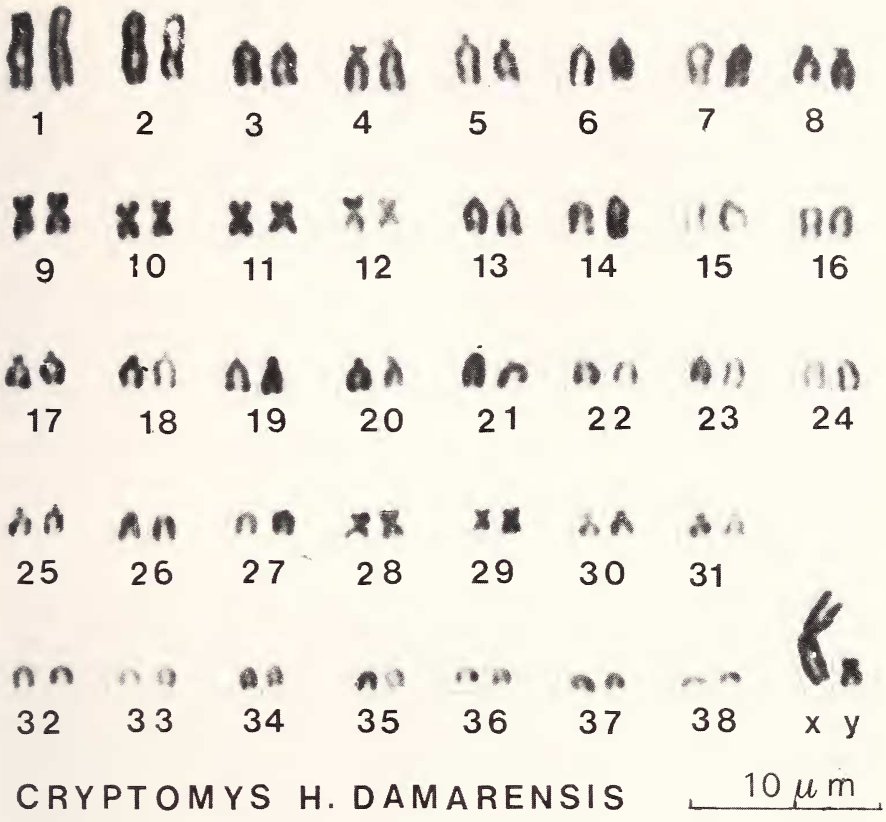

Fig. 11. Karyotype of *Cryptomys hottentotus damarensis* (specimen from Kalahari desert) displaying 78 chromosomes. Notice the considerable amount of acrocentric chromosomes which actually diversify the complement of this subspecies (or species?) from those of *C. h. hottentotus* and *C. h. natalensis*

number 2n = 60. She concluded that fossorial rodents fall into two categories: those with conservative karyotypes like the Bathyergidae and Octodontidae (i.e. based on the chromosomal uniformity and low taxonomic diversity of *Spalacopus cyanus,* 2n = 58, FN = 116), and those with variable karyotypes like Geomyidae, Spalacidae and Ctenomyidae.

The results of the present paper do not support the idea that bathyergids are indeed karyotypically conservative. We found diversification in diploid numbers (2n = 54, 56, 74, 78) as well as in karyotype morphology. We will discuss our findings as follows: karyotype variability between species of the same genus, karyotype variability between "subspecies" within a species and differences in karyotype morphology.

Interspecific karyotype variability between species of the same genus

Bathyergus janetta and *B. suillus* have different diploid numbers, namely 2n = 54 and 2n = 56 respectively. This variation, as will be discussed in detail later, is derived from the rearrangement of some karyotype components: 1. *B. suillus* has 2 pairs of medium sized acrocentrics absent in *B. janetta,* 2. *B. suillus* has one small acrocentric pair carrying a NOR region, whereas *B. janetta* has two NORs carried by two pairs of metacentrics.

Karyotype variability between "subspecies" within a species

The three subspecies of *Cryptomys hottentotus* studied here, i.e. *C. h. hottentotus, C. h. natalensis* and *C. h. damarensis* have the following diploid numbers: 2n = 54, 54, and 74 as well 78, respectively. Obviously *C. h. damarensis* varies drastically in karyotype in comparison with the other two subspecies.

Williams et al. (1983) karyotyped 9 *Cryptomys foxi* from Cameroons and found that within the same populations 8 had a diploid number 2n = 66 and one female 2n = 70. *Cryptomys foxi* which is undoubtedly a different species from the South African *Cryptomys,* shows a karyotype which is more similar to *C. h. hottentotus* than to *C. h. damarensis.* Since only two individuals of *C. h. damarensis* have been karyotyped in this study, and each displayed different diploid numbers, i.e. 74 and 78, future studies will be needed to discover whether *C. h. damarensis* is polymorphic or polytypic. Karyotypic differences in morphology were also evident between *C. h. natalensis* and *C. h. hottentotus.* These probably involve pericentric inversions. We have no data, for this species, on meiotic disturbance due to the structural heterozygosity of these inversions in putative hybrids. However, these chromosomal inversions do separate these two subspecies, and our allozyme evidence (Nevo et al. 1985) indicates that they, as well as *C. h. damarensis,* are widely separated and deserve specific recognition.

Karyotype differences in morphology

Even in the instances where species or genera display the same diploid number of 2n = 54, as in *Bathyergus janetta, Cryptomys hottentotus* and *Georychus capensis,* the species vary in karyotype morphology due to chromosomal rearrangements. For example, there are no acrocentrics in *B. janetta,* one pair in *C. hottentotus* and two pairs in *G. capensis.* Unfortunately our G-bands do not permit a reliable comparison of homologous elements between species, firstly because of the small size of the chromosomes characterizing bathyergids in general, and secondly because of the differential condensation and shortness due to the bone marrow method. A successful G-band comparison is possible, however, between the largest submetacentric, chromosome no. 1 in all karyotypes. The comparison (Fig. 12) reveals homologous banding in all species, excepting *C. hottentotus natalensis* where the short arm appears to be longer than in other species.

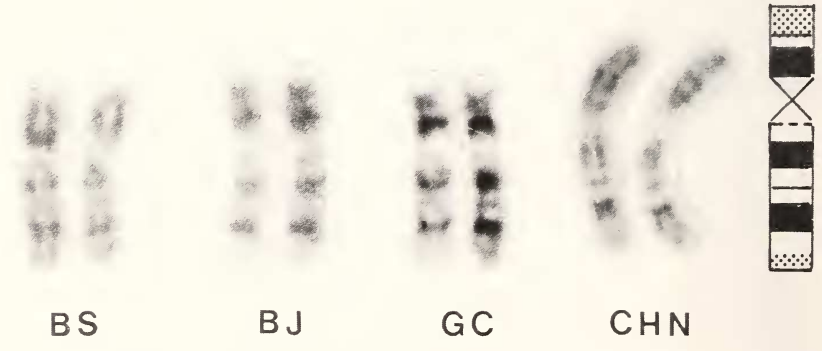

Fig. 12. A comparison of the G-band pattern between chromosomes no. 1 (the longest submetacentrics) of *Bathyergus suillus* (BS), *B. janetta* (BJ), *Georychus capensis* (GC) and *Cryptomys h. natalensis* (CHN). The band sequences correspond in all species; a larger terminal band is displayed by *C. h. natalensis*

A comparative analysis of C-bands also reveals intergeneric and interspecific karyotype differences. *Cryptomys* and *Georychus* display different distributional patterns of the heterochromatic blocks (Fig. 8). Karyotype differences are also displayed by the heterochromosomes. The Y-chromosome is acrocentric in all species; however the X-chromosome is metacentric in *Bathyergus* and *Georychus* (centromeric index, c.i. = 50), but submetacentric in *C. h. hottentotus* and *C. h. natalensis* displaying a c.i. of 26 and 34, respectively. This variability in the X-chromosome is remarkable in view of the general conservatism of X-chromosomes in mammals.

Karyotype evolution

Discussion of karyotype evolution in the bathyergids would be premature. However, one could tentatively suggest a preliminary phylogenetic outline based on two assumptions. First, if the most common pattern (i.e. the most widely shared morphological feature) indeed represents the most primitive state of the group, then 2n = 54 should be considered the primitive state. Second, one NOR-chromosome pair is also regarded as the primitive state. Based on these two assumptions, we tentatively propose the following evolutionary scheme considering both the NOR-chromosome and the subtelocentrics of *B. suillus:*

a. the ancestral 2n = 54 karyotype involves 2 pairs of small acrocentrics, one being nucleolar
b. one fusion between these acrocentrics decreased the diploid number to 2n = 52, giving rise to a small NOR metacentric
c. duplication of the NOR metacentric pair led to the karyotype evolution of *Bathyergus janetta,* which consists of 2n = 54 and two pairs of NOR metacentrics (which are indeed similar morphologically)
d. a Robertsonian fission of the ancestral karyotype 2n = 54 changed a metacentric into two acrocentrics, leading to the 2n = 56 of *B. suillus*
e. a large number of further chromosome rearrangements were involved in the evolutionary divergences of *Bathyergus, Cryptomys* and *Georychus.*

Our preliminary observations clearly indicate that the Bathyergidae are not karyotypically conservative as suggested on the basis of two bathyergid species, i.e. *Heterocephalus glaber* and *Heliophobius argenteocinerus* (George 1979).

Finally, a last comment on the karyotypic evolution in the bathyergid across Africa. Our knowledge is yet immature for a continental appraisal of bathyergid karyotypic evolution, hence this comment is a pure speculation. If 2n = 54 was indeed the ancestral karyotype in bathyergids, then bathyergids possibly originated in southern Africa. From their origin bathyergids could have then evolved in two directions northeastwards and, northwestwards, into drier ecological environments in Kenya and Somalia on the one hand and in Namibia and the Kalahari desert on the other. Noteworthy, the diploid chromosome numbers increase in both directions. Diploid number increased northeastward from 2n = 54 to 2n = 60 in *Heterocephalus glaber* (George 1979; Capanna and Merani 1980) and in *Heliophobius argenteocinereus* (George 1979), and also increased northwestward to 2n = 74 and/or 78 in *Cryptomys damarensis.* The increase in diploid numbers involves a higher recombination index which may provide a higher adaptive chromosomal diversity to increasingly uncertain and climatically fluctuating environments. A similar situation, on a much smaller scale, was found in the *Spalax ehrenbergi* superspecies of subterranean mammals in Israel where 4 chromosomal species (2n = 52, 54, 58 and 60) are progressively adapted to increasingly unpredictable climates. A similar pattern of increasing heterozygosity towards the climatically unpredictable steppes has been described in Israel for many unrelated species involving plants, invertebrates and vertebrates (Nevo 1983).

A canalization model of adaptive chromosomal evolution has been suggested by Bickham and Baker (1979). Their model implies that the karyotype is a significant aspect

in the adaptive strategy of the organism, and that for each adaptive zone there is an optimum karyotype that can be evolved by chromosomal rearrangements. After evolution of the optimum, additional karyotypic evolution will be then primarily by genic and molecular mechanisms. We now have allozymic evidence, based on 20 putative gene loci (Nevo et al. 1985), supporting this thesis. Furthermore, our allozymic evidence indicates that speciation was indeed prolific in the South African Bathyergidae. This may be associated with the dramatic speciation of plants in South Africa comprising 18,500 species in 1,930 genera (Goldblatt 1978), many of which are bulb and corn plants which comprise the major food items of subterranean rodents.

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Zusammenfassung

Differenzierung der Karyotypen bei bodenbewohnenden Sandgräbern (Bathyergidae, Rodentia) Südafrikas

Untersucht wurden die Karyotypen der 4 südafrikanischen Sandgräber (Bathyergidae) *Bathyergus janetta, B. suillus, Georychus capensis* und *Cryptomys hottentotus.* Von der letzten Art wurden Individuen verglichen, die drei unterschiedlichen Unterarten zugeordnet werden können: *C. h. hottentotus, C. h. natalensis* und *C. h. damarensis.* Ausgewertet wurden somatische Metaphasen aus dem Knochenmark und Meiose-Präparate aus den Hoden. Die G-, C- und NOR-Bandenmuster wurden analysiert, um die Vergleichsmöglichkeiten der Karyotypen der einzelnen Arten steigern zu können. *C. h. hottentotus* und *C. h. natalensis* besitzen einen ähnlichen Karyotyp mit 2n = 54 Chromosomen, doch konnten in der Morphologie von zwei Chromosomenpaaren Unterschiede zwischen den beiden Formen nachgewiesen werden. Dagegen ist der Karyotyp von *C. h. damarensis* völlig verschieden. Von den zwei untersuchten Tieren besaß das eine aus dem Nordwesten Südafrikas 2n = 74, das zweite aus der Kalahari-Wüste 2n = 78 Chromosomen. *Bathyergus janetta* besitzt eine diploide Zahl von 2n = 54, *B. suillus* dagegen von 56. Auch die Zahl und die Morphologie der Chromosomen mit NOR-banden ist bei den beiden kongenerischen Arten unterschiedlich. Bei *Georychus capensis* konnte die diploide Zahl von 2n = 54 bestätigt werden, wie sie schon Matthey (1956) beschrieb. Diese Ergebnisse zeigen, daß die am häufigsten auftretende – und daher wohl auch als ursprünglich anzunehmende – 2n-Zahl 54 beträgt. Die Bathyergidae weisen eine zwischen- und innerartliche Differenzierung der Karyotypen auf, die sie nicht als zytogenetisch konservativ, sondern ganz im Gegenteil als in aktiver Artbildung begriffen ausweist, bei der eine chromosomale Vielfalt beteiligt ist.

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WISSENSCHAFTLICHE KURZMITTEILUNGEN

Behaviour and orientation of a released Pine marten *(Martes martes)*

By E. Pulliainen

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According to the familiar area hypothesis, animals tend to become familiar with their surroundings and having learned to do so tend to move within this familiar area (Pulliainen 1974; Baker 1978, 1982). The present author's previous field studies on the pine marten (*Martes martes* L.) have suggested that frequent scent-marking may play a considerable part in the orientation of an individual of this species within its home range

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